

REPRODUCTION OF THE RED-COCKADED WOODPECKER IN CENTRAL FLORIDA

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ABSTRACT.—Red-cockaded Woodpeckers (*Picoides borealis*) near the southern extreme of the species' range had a low fledging rate, high fledgling survivorship, and high level of breeder experience and adult survivorship compared to other populations. Breeding male and female survivorship was 10% and 23% higher, respectively, than northern populations. Tenure of helpers was higher than other populations, apparently as a result of high adult survivorship. The frequency of female helpers was higher (30%) than reported for other populations (5%). Group size ranged from two to five members and averaged 2.4 birds prior to nesting. Reproduction in central Florida was lower than other populations (1.0 vs 1.6 fledglings per group). Experienced pairs without a helper produced significantly more fledglings than experienced pairs with a helper (1.45 and 0.87 fledglings/group, respectively). Reproductive success was correlated with breeder experience, outside intrusion rate, and territory size. Received 27 June 1990, accepted 1 Nov. 1991.

Red-cockaded Woodpeckers (*Picoides borealis*) breed cooperatively in groups of two to six adults. One breeding pair within each group lays a single clutch (Ligon 1981, Lennartz et al. 1987, Walters et al. 1988). Breeding success probably is affected by the level of disruption due to the intrusion of alien Red-cockaded Woodpeckers, as well as age and breeding experience and possibly habitat quality (Ligon 1981, Lennartz et al. 1987). In central Florida, territories are larger with very little extra-territorial habitat. In northern populations, territories are smaller with substantially more extra-territorial habitat (Hooper et al. 1982, Repasky 1984, Blue 1985, Porter and Labisky 1986, DeLotelle et al. 1987).

Habitat differences between populations could affect demographics, social dynamics, and reproductive success. We examined the effect of such differences in the present study in order to (1) document demography and social dynamics in this population, (2) develop a model of the influence of social and habitat factors on reproductive success, and (3) compare demography and social dynamics between populations.

METHODS

The 1328-ha study area, the Curtis H. Stanton Energy Center, is 21 km southeast of Orlando, Florida. The habitat was dominated by longleaf pine (*Pinus palustris*) with an understory of saw palmetto (*Serenoa repens*) (<1 m) and very few hardwoods, interspersed cypress domes, bayheads, and wet prairies (DeLotelle et al. 1983, DeLotelle et al. 1987).

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Pine habitat occurred in distinct stands of varying ages and densities. Pine tree characteristics were based on aerial photographs and 25 field-inspected plots for dbh, density, age, and basal area.

The study area was searched annually for nesting and roosting trees. Eleven Red-cockaded Woodpecker groups were studied from the late summer of 1980 through the fall of 1987. These 11 groups were part of a larger population of an additional 26 groups in similar pine habitat surrounding the study area. Birds were captured by placing mist netting on a wire frame over the entrance to roost cavities during mornings and evenings and banded with color-coded plastic leg bands and U.S. Fish and Wildlife Service identification bands. The banding frequencies for all group members during the post-fledging and fall/winter observation periods were 83% ($N = 120$ bird-years) and 96% ($N = 128$ bird-years), respectively. During nesting, 95% ($N = 85$ bird-years) of group members were banded. Roost trees for individuals ($N = 131$) were determined during banding activities, territorial monitoring studies ($N = 95$ days), and seasonal censusing ($N = 16$ days). Cavity tree locations for each group were plotted on aerial photographs (1:4800) and the location of roosting birds recorded. During the post-fledging periods all unbanded birds in the group counts were fledglings. For the two years of no reproductive observations (1983 and 1986), two additional summer censuses, including banding activities, were conducted to establish group composition.

Each group was monitored during the four seasons (winter and spring only in 1985) for composition, breeder replacement, and intruder frequency. The reproductive survey included a 1–3 h weekly census of each group to determine composition and participation of individuals in nesting activities. Group composition was determined by observing band combinations on individual birds during daily foraging trips ($N = 215$ days), nesting activity ($N = 69$ days), and other behavioral censuses ($N = 30$ days). Sampling usually began as the birds started their daily activity and included a record of observation time. Both the behavior of new birds interacting with residents of a territory and the behavior of group members during interactions with neighboring groups were recorded during 1909 h of observation.

Individual males and females were assigned breeding status if they were present as a pair only on the territory. For the other groups with helper males, breeding status was assigned to the male in whose roost tree nesting occurred ($N = 27$) (see Walters 1990). For one group with a female helper, copulation was observed between the breeding male and the female that was assigned breeding status. In the other group with a female helper, breeding status was assigned to the female that appeared to dominate the other female at foraging sites. Subsequently, breeding status was assigned to males and females that had previously resided on a territory as breeders. Of the 35 group-years, the breeding status of 24 of the male bird-years and 31 of the female bird-years was assigned by virtue of being the only male or female present in the group. Breeding status was also verified based on observed copulations ($N = 5$ pairs). Five of the helpers were banded as fledglings on their natal territory. Survival and turnover frequencies for seven years were calculated by comparing the censuses of banded birds tabulated from one year to the next.

Intruder status, which included helpers, displaced breeders, floaters, and birds of unknown status, was assigned to any Red-cockaded Woodpecker observed on a territory in which it was not a member of the resident group. Helper status was assigned to birds, other than breeders, occurring on territories for more than one year that had little or no overt agonistic interaction with other group members and participated in nesting activities and inter-group territorial interactions. Displaced breeders were known breeders that were subsequently observed in other territories after their replacement. Floaters were banded birds with no observed previous breeding history that were observed on two or more territories in a survey year and were not regularly associated with any single group. Floaters were followed from their roost cavities on seven occasions. The behavioral interactions between residents and intruders were later standardized to an 11.5-h sampling day.

Thirty-five group years of reproductive observations were compiled. Visual inspections of nest trees were made weekly during April and May and more frequently thereafter depending on nestling development. During 1981, fledging rates were determined by counting group members weekly during nesting and recounting group members and fledglings during the fledging process. Based on behavior, all fledgling censuses during 1981 were conducted within one to three days of fledging (Jerauld et al. 1983). Thereafter (1982, 1984, 1985, 1987), cavity contents of nest trees were recorded weekly or more often during April through July with the aid of a mirror and a flashlight. Ninety-three cavities were inspected for occupancy by other wildlife species, including 60% and 95% of completed cavities for 1985 and 1987, respectively. Feeding rates for individual adults were compiled throughout the day for nests of 10-day and older nestlings and for fledglings.

Annual territory sizes were measured in 1981–1984 ($N = 6$ territories) and 1986–1987 (two previous territories and five previously un-sampled territories). Movements of groups were recorded at five minute intervals on photocopies of aerial photographs (scale 1:4800) for a total of 1647 h following methods described by DeLotelle et al. (1987). Groups were generally followed from the morning to well into the late afternoon. On occasion, groups were followed all day or from noon until roosting (23 of 215 days). Territory size and configuration were based on a modified minimum polygon procedure, connecting points of territorial interaction and areas of repeated use where no interactions were observed (Hooper et al. 1982). Territories not measured (7 of 35 group-years) were estimated from figure 1 of DeLotelle et al. (1987). Nesting home ranges, based on an additional 146 h of observing daily foraging, were determined for six territories during the nestling stage. Areas for those nesting home ranges not measured were taken to be a 46.5-ha circle around the nest tree.

A multiple regression model (SAS Institute 1985) was constructed of reproductive success versus breeder experience, group size, habitat quality index, annual territory size, and intrusion rate. Breeding success categories were no eggs laid (1), eggs laid but not hatched (eggs only) (2), one successful fledgling (3), and two or more successful fledglings (4) (van Riper 1984). Breeder experience levels were: no previous experience, one member with experience, and both members experienced (Lennartz et al. 1987). Group size was either a breeding pair without a helper or a pair with one (male or female) helper. The habitat quality of the nesting home range was evaluated by mean age and density of pine for the territories of each group-year (Equation 1, DeLotelle et al. 1987). Habitat quality influences group size (Brown and Balda 1977), and foraging habitat preference as a quality index has been used in other Red-cockaded Woodpecker studies (Lennartz et al. 1987). Intruder rates were standardized to a field effort of an 11.5-h day. The number of intrusions for each group-year was divided by the standardized sampling effort.

RESULTS

Group composition and survivorship.—Red-cockaded Woodpecker groups consisted of two to five individuals. There were 20 group-years (57%) for pairs without a helper and 15 (43%) for pairs with a helper. Group size ($N = 35$ group-years) prior to the nesting season was 2.4 ± 0.5 (SD) birds and increased to 3.4 ± 0.9 after nesting to include 29% fledglings. The mean group size during the winter was 3.1 ± 0.8 birds ($N = 41$ group-years) and consisted of 65% breeders, 25% non-adults and 10% helpers with more than one year of experience. Females comprised 30% of the helpers and were present during the first four study years, but not the latter three years.

Annual retention of individual breeders on resident territories was $84\% \pm 18$ ($N = 48$) and $81\% \pm 21$ ($N = 48$) for males and females, respectively. Survivorship in the study area for breeding males and females was 90% and 93%, respectively, assuming birds that disappeared from the study area died. Helpers continued in that status on their resident territories for a mean duration of at least 2.2 ± 0.7 years ($N = 10$) (2.0 years for females and 2.3 years for males). Based on the non-adult component of the mean post-fledging and mid-winter group size (1.0 and 0.73 birds, respectively), the seven-month juvenile survivorship in the population was 73%.

Territorial interactions and intrusion.—Breeders and male and female helpers were observed participating in inter-group conflicts and expulsion of intruding groups. Interactions between residents and non-residents occurred as a result of the inter-territorial movements of helpers, male and female floaters, and displaced breeders (Table 1). The 0.7 ± 0.3 intrusions per day by these birds were in addition to the 0.5 ± 0.3 inter-group conflicts per territory-day. While female floaters accounted for 4% of the population during nesting and 9% during winter, they were observed in every territory and their movements accounted for 27% of the intrusions. About one-third of female floater intrusions resulted in little response from residents while about one-third were aggressively expelled and involved interaction with the breeding pair. Female floaters and other alien birds were observed to roost ($N = 6$) and forage in territories while remaining un-associated with the resident group.

Helper males and helper females accounted for 11% of all intrusions into surrounding territories (Table 1). On five occasions, a helper male foraged on a neighboring territory in association with a female floater, and on one occasion with a helper female on her territory. Two female helpers which had been in that status for two and three years, respectively, were observed in several territories before displacing a breeding female. Helper males and females, however, were consistently observed foraging with their resident group with little or no overt negative interactions with the resident breeders and participated in inter-group territorial interactions.

Displaced breeders accounted for 9% of all intrusions. The majority of displaced breeding females were observed foraging in loose association with resident groups. Four displaced breeders, however, eventually attained breeding status, three outside of the study area. In a one year period, a chain of displaced and replaced breeding females occurred on three different territories in succession.

Prolonged and persistent interaction between one member of a breeding pair and an intruder was observed on four territories. The conflicts consisted of aerial chases and displacements on trees between the alien bird

TABLE 1
FREQUENCY OF GROUP/INTRUDER BEHAVIORS BY INTRUDER STATUS DURING TERRITORY AND NEST MONITORING FOR 11 GROUPS (M = MALE;
F = FEMALE)

Behavior	Intruder status										Rate ^b
	Helper		Floater		Breeder		Displaced breeder		Unknown ^a	Total	
	M	F	M	F	M	F	M	F			
Loose association	2	1	5	14	—	1	1	8	26	58	0.35
Foraging ^d	6	1	—	5	—	—	—	—	—	12	0.08
Interactions	1	2	—	3	—	—	—	2	11	19	0.11
Intruder expulsion	—	—	—	9	—	1	—	—	17	27	0.16
Total	9	4	5	31	0	2	1	10	54	116	0.70
Breeder ^c replacement	1	2	—	2	—	—	1	3	7	16	

^a Unbanded, or color bands not observed.

^b Number of intruders per 11.5-h day.

^c Three of these breeder replacements occurred outside study area.

^d Helper and floater foraging together.

and a specific breeder. In two cases the group included a helper although the intruder was of the opposite sex. The helper and other breeder had little involvement in the interactions. Two of the displaced breeders (a male and a female) were later observed as breeders on other territories. Competition involving aerial chases and spiral chases on trees was also observed between a displaced breeding female and a former female helper (from another group) for a third female's breeding position.

Nesting and helping behavior.—Clutch size averaged 2.9 ± 0.8 eggs, with a mean laying date of May 13 ± 17 days, and was significantly ($t = 5.4$, $P < 0.001$) larger for experienced (3.3 ± 0.4 eggs, $N = 12$) than for inexperienced (1.8 ± 0.5 eggs, $N = 4$) females. Egg incubation was performed by all group members. Nesting home ranges averaged 46.5 ± 23.7 ha ($N = 6$) and contained a mean of 4237 ± 2293 pine stems, with a mean age of 72 ± 20.6 years and a mean dbh of 20.3 ± 2.6 cm.

Both parents fed nestlings, males accounting for 56% and females 44% of trips to the nest ($N = 903$). Female helpers were often observed feeding nestlings and fledglings, but no frequency data were collected relative to that. Fledgling feeding through September was 7.8 visits/h, declining in October to 2.0 visits/h. During June, fledgling (five male and one female) feeding was performed primarily (94%, $N = 534$ feedings) by the breeding male. One-year-old helpers were not observed feeding fledglings during the first month after fledging. While foraging, the one-year-old helper (three males and one female) reacted negatively when approached on a tree by the fledgling, often resulting in extended flight movements and vocalization by all group members. By mid-August, one-year-old helpers accounted for 19% of feeding visits to fledglings. Second-year and older helpers commenced feeding fledglings shortly after the young fledged.

Breeding success.—Eggs were laid in 31 (89%) of the 35 group-years. Nestlings were observed in 26 (84%) of these 31 nesting group-years. Of these 35 group-years, only eight included the same group structure as in previous years due to breeder turnover and the presence or absence of helpers. For pairs without a helper, 43% ($N = 3$) of the unsuccessful nests were egg failures while 57% ($N = 4$) were no nesting attempt. For pairs with helpers, all nest losses ($N = 2$) were egg failures. Four of the five nest failures occurred in groups with one or both breeders inexperienced. No competitors or predators were observed in or near the nest cavities at the time of egg loss, and breeding males were observed roosting in the nest cavities one to seven days later. In addition, 93 cavity inspections for predators and competitors revealed that 6% were occupied by other bird species, including Red-bellied Woodpeckers (*Melanerpes carolinus*, 3%), Eastern Bluebirds (*Sialia sialis*, 2%), and un-identified nestlings (1%). Wasps were found in 7% of the cavities.

TABLE 2

REGRESSION COEFFICIENTS OF BREEDING SUCCESS VERSUS MEAN BREEDER EXPERIENCE, HABITAT QUALITY INDEX, GROUP SIZE, TERRITORY SIZE, AND LEVEL OF INTRUSION

Parameter	Coefficient \pm SE	P
Intercept	-1.359 ± 0.876	
Experience	1.586 ± 0.293	<0.001
Habitat quality	0.041 ± 0.023	0.086
Group size	-0.069 ± 0.212	0.749
Territory size	0.015 ± 0.005	0.008
Intrusion	-2.325 ± 0.734	0.005

The fledging rate per group was 1.0 ± 0.8 ($N = 35$ group-years). Successful nesting by pairs without a helper (1.54 ± 0.69 , $N = 13$) produced significantly ($t = 2.21$, $df = 25$, $P = 0.039$) more fledglings than pairs with helpers (1.08 ± 0.29 , $N = 13$). Fledging rates were similar among groups whether they had a male or female helper. In the cases where both breeders were experienced, pairs without a helper produced significantly ($t = 2.12$, $P = 0.046$) more fledglings (1.45 ± 0.82 , $N = 11$) than pairs with a helper (0.87 ± 0.33 , $N = 8$). This result is more striking since the mean experience-years of male and female breeders for 1984 and later years, an index to age, was slightly higher for pairs with a helper (3.8 and 2.7 years, $N = 6$) than for pairs without a helper (3.4 and 2.6 years, $N = 7$). Additionally, three groups composed of the same experienced male had mean fledging rates of 0.75 with and 1.4 without a helper in different years.

The level of reproductive success (no eggs, eggs only, one fledgling, and two or more fledglings) was correlated significantly ($R^2 = 0.76$, $P < 0.0001$, $N = 25$) with breeder experience, intrusion rate, and territory size (Table 2). The magnitude of the regression slopes suggests that reproductive success is most responsive to level of intrusion and secondarily to breeder experience.

DISCUSSION

Demographic characteristics of the central Florida population include high level of breeder experience, high adult survivorship, high frequency of successful nests, low fledging rate, and high fledgling survivorship as compared to other populations (Lennartz et al. 1987, La Branche 1988, Lennartz and Heckel 1988, Walters et al. 1988). Annual retention of male and female breeders on resident territories (84 and 81%, respectively) is higher than in North Carolina (73 and 56%), South Carolina (78 and

68%), and Georgia (72 and 51%) populations (Lennartz and Heckel 1988, Walters et al. 1988). The percentage of successful nests in central Florida (84%) appears lower than in South Carolina (93%) but higher than in either the Georgia (69%) or North Carolina (72%) populations. In sharp contrast to results from other populations, central Florida groups with helpers fledged nearly one bird less per group than either the South Carolina or North Carolina populations (0.9 vs 2.05 and 1.99, respectively). Groups without helpers produced only 0.4 fewer fledglings than the northern populations (1.4 South Carolina and 1.38 North Carolina, respectively). The overall differences in breeding success between central Florida and northern populations (1.0 and 1.6 fledglings/group, respectively) would be expected to be much smaller given the high experience level of breeders and reduced nest competition from other species in central Florida.

Social structure and behavior.—The proportion of groups with helpers was 43% compared to 46% and 30% for South Carolina and North Carolina, respectively. Female floaters accounted for 4% to 9% of the population compared to an apparently smaller percentage in North Carolina. Group social structure was similar to other populations but included a greater percentage of female helpers.

A higher frequency of intrusion by females searching for breeding vacancies should occur because of the different dispersal strategies employed by male and female Red-cockaded Woodpeckers (Walters et al. 1988). Female floaters accounted for 50%, and other female classifications for 26%, of banded bird intrusions within territories (Table 1). The frequency of interactions generated by the movement of these birds through neighboring territories and other inter-group interactions appear to be substantially higher in central Florida (1.2 and 0.8 conflicts/day, respectively) than for North Carolina (Repasky 1984, Blue 1985). The replacement and subsequent movement of female breeders appeared to be the result of competition more often in central Florida than in North Carolina, where most such movements follow loss of the mate (Walters et al. 1988).

Demographics and social structure.—Given the relatively low reproductive rate in central Florida, it might be expected that the frequency of helpers would be lower than in other populations. In central Florida, helper tenure for males is higher (2.2 vs 1.6 years, respectively) than in other populations (Fig. 3.9, Walters 1990). The dispersal options of young birds may be reduced in central Florida because of reduced availability of breeding positions (Fig. 3.2, Brown 1987). A 30% female helper frequency in central Florida compared to 5% in both South Carolina and North Carolina, where turnover rates of adult females are greater, further supports the hypothesis of social dynamics being altered by adult survivorship. Dispersing females, with breeding positions scarce, are more

likely to end up as floaters or remain on the natal territory. Those females that do disperse and attain breeding status are more likely to do so through aggressive interaction with an established breeder.

It is noteworthy that in central Florida, experienced pairs with a helper produced significantly ($P < 0.05$) fewer fledglings than experienced pairs without a helper (0.87 and 1.45, respectively). A similar negative or non-positive effect of group size on reproduction has been reported for the Jungle Babbler (*Turdoides striatus*) and Green Woodhoopoe (*Phoeniculus purpureus*) (Gaston 1978, Ligon 1981). Pairs with a helper should have produced significantly more fledglings given the relatively high experience level of the breeding pair. There may be some negative interaction occurring between the pair and the helper that is more pronounced in low pine stocking habitat. Interference and competition involving breeder-helper conflicts occur in other cooperative breeders and may not involve overt aggression (Zahavi 1974, Emlen 1982, Mumme et al. 1983, Hannon et al. 1985).

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LITERATURE CITED

- BLUE, R. J. 1985. Home range and territory of Red-cockaded Woodpeckers utilizing residential habitat in North Carolina. M.S. thesis, North Carolina State Univ., Raleigh, North Carolina.
- BROWN, J. L. 1987. Helping and communal breeding in birds: ecology and evolution. Princeton Univ. Press, Princeton, New Jersey.
- AND R. P. BALDA. 1977. The relationship of habitat quality to group size in Hall's Babbler (*Pomatostomus halli*). *Condor* 79:312–320.
- DELOTELLE, R. S., R. J. EPTING, AND J. R. NEWMAN. 1987. Habitat use and territory characteristics of Red-cockaded Woodpeckers in central Florida. *Wilson Bull.* 99:202–217.
- , J. R. NEWMAN, AND A. E. JERAULD. 1983. Habitat use by Red-cockaded Woodpeckers in central Florida. Pp. 59–67 in *Red-cockaded Woodpecker Symposium II proceedings* (D. A. Wood, ed.). Florida Game Fresh Water Fish Comm., Tallahassee, Florida.
- EMLEN, S. T. 1982. The evolution of helping. II. The role of behavioral conflict. *Am. Nat.* 119:40–53.
- GASTON, A. J. 1978. Demography of the Jungle Babbler (*Turdoides striatus*). *J. An. Ecology* 130:654–676.
- HANNON, S. J., R. L. MUMME, W. D. KOENIG, AND F. A. PITELKA. 1985. Replacement of

- breeders and within-group conflict in the cooperative breeding Acorn Woodpecker. *Behav. Ecol. Sociobiol.* 17:303–312.
- HOOPER, R. G., L. G. NILES, R. F. HARLOW, AND G. W. WOOD. 1982. Home ranges of Red-cockaded Woodpeckers in coastal South Carolina. *Auk* 99:675–682.
- JERAULD, A. E., R. S. DeLOTTELLE, AND J. R. NEWMAN. 1983. Restricted Red-cockaded Woodpecker clan movement. Pp. 97–99 in *Red-cockaded Woodpecker Symposium II proceedings* (D. A. Wood, ed.). Florida Game Fresh Water Fish Comm., Tallahassee, Florida.
- LA BRANCHE, M. S. 1988. Reproductive ecology of the Red-cockaded Woodpecker in the sandhills of North Carolina. M.S. thesis, North Carolina State Univ., Raleigh, North Carolina.
- LENNARTZ, M. R. AND D. G. HECKEL. 1988. Population dynamics of a Red-cockaded Woodpecker population in Georgia piedmont loblolly pine habitat. Pp. 48–55 in *Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium* (R. R. Odum, K. A. Riddleberger, and J. C. Ozier, eds.). Georgia Dept. Nat. Res., Game and Fish Div., Athens, Georgia.
- , R. G. HOOPER, AND R. F. HARLOW. 1987. Sociality and cooperative breeding of Red-cockaded Woodpeckers (*Picoides borealis*). *Behav. Ecol. Sociobiol.* 20:77–88.
- LIGON, J. D. 1981. Geographic patterns and communal breeding in the Green Woodhoope, *Phoeniculus purpureus*. Pp. 231–243 in *Natural selection and social behavior: recent research and new theory* (R. D. Alexander and D. W. Tinkle, eds.). Chiron Press, New York, New York.
- MUMME, R. L., W. D. KOENIG, AND F. A. PITELKA. 1983. Mate guarding in the Acorn Woodpecker: within-group reproductive competition in a cooperative breeder. *An. Behav.* 31:1094–1106.
- PORTER, M. L. AND R. F. LABISKY. 1986. Home range and foraging habitat of Red-cockaded Woodpeckers in northern Florida. *J. Wildl. Manage.* 50:239–247.
- REPASKY, R. R. 1984. Home range and habitat utilization of the Red-cockaded Woodpecker. M.S. thesis, North Carolina State Univ., Raleigh, North Carolina.
- SAS INSTITUTE. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, North Carolina.
- VAN RIPER, III, C. 1984. The influence of nectar resources on nesting success and movement patterns in the Common Amakihi (*Hemignathus virens*). *Auk* 101:38–46.
- WALTERS, J. R. 1990. The Red-cockaded Woodpecker: a "primitive" cooperative breeder. Pp. 67–102 in *Cooperative breeding in birds: long-term studies of ecology and behavior* (W. D. Koenig and P. B. Stacy, eds.). Cambridge Univ. Press, Cambridge, U.K.
- , P. D. DOERR, AND J. H. CARTER, III. 1988. The cooperative breeding system of the Red-cockaded Woodpecker. *Ethology* 78:275–305.
- ZAHAVI, A. 1974. Communal nesting by the Arabian Babbler. *Ibis* 116:84–87.